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Skeletal morphometry of *Millepora* occurring in Brazil, including a previously undescribed species

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Abstract.—The aims of this study were to identify the species of *Millepora* occurring in Brazil and compare the skeletal morphology of *M. braziliensis* from Brazil and *M. squarrosa* from the Caribbean (to address confusion over their synonymy). One hundred and three colonies of *Millepora* were collected from various sites along the Brazilian coast. In an attempt to facilitate delineation among species, diameters of the gastropores and dactylopores were compared in addition to other morphological characters. We proposed that the colonies collected from Brazil comprised four species: *M. alcicornis* (34 colonies), *M. braziliensis* (45), *M. nitida* (13), and one previously undescribed species (11). Analyses of variance of the diameters of gastropores and dactylopores among the various species showed considerable intra-specific variability and some inter-specific spatial variation. At the Abrolhos Islands, significant differences were detected between *M. alcicornis, M. braziliensis* and *M. nitida* for the mean diameter of the dactylopores, but not the gastropores. In contrast, significant differences in mean diameter of the gastropores were detected between *M. braziliensis* and *M. alcicornis* across three other locations. We hypothesized that Caribbean *M. squarrosa* is a species distinct from *M. braziliensis,* although the use of molecular systematics may be required to eliminate doubts about their synonymy.

The genus *Millepora* comprises 17 valid species, globally distributed throughout tropical oceans and generally down to depths less than 40 m (Cairns et al. 1999). Of the species currently described, eight occur in the Indian Ocean, nine in the western and central Pacific Ocean, four in the eastern Pacific Ocean, and six in the western Atlantic Ocean (Cairns et al. 1999). Since they often form an integral component of reef structures, *Millepora* is considered important to the ecology of reef systems throughout their distributions (Lewis 1989, Edmunds 1999). Despite this and their abundance, compared to scleractinians there is little information available on their ecology and life histories. Lewis (1989) attributed this in part to their relatively lower diversity and less spectacular growth forms, although perhaps the main contributing factor concerns the difficulties associated with taxonomy and distinction among the various species.

Historically, there have been many problems associated with the identification of *Millepora* (see Dana 1846; Quelch 1884, 1885, 1886; Hickson 1891, 1897, 1898a, 1898b, 1899, 1900; Duerden 1899). Their identification predominately has been based on the morphology of gastropores and dactylopores (Boschma 1948a, 1948b, 1949a, 1949b, 1950, 1956, 1961, 1962, 1964, 1966, 1968), in addition to gross skeletal characters (e.g., colony growth form) traditionally used to separate scleractinians (Vaughan & Wells 1943; Fishelson 1973; Amaral 1991, 1994; Gattuso et al. 1991). There is, however, considerable disagreement over appropriate homologous characters that might be used to facilitate identification. For example, Hickson (1898a) suggested that important characters include: colony form, size of the pores and their degree of isolation, presence or absence of ampullae, texture of the colony surface, relative number of dactylopores and gastropores, and anatomy of the soft parts. Boschma (1948a) questioned many of these variables and postulated that growth form, although often highly variable, was the only character that could be used for positive identification. In later studies, Boschma (1949a, 1950) indicated that size and form of the ampullae could also have taxonomic value. Similarly, Weerdt (1981, 1984) and Lewis (1989) suggested that, except for growth form and attributes of the gastropores and dactylopores, there are few characters of taxonomic value. This is primarily because each species often has highly variable phenotypic forms (Stearn & Riding 1973; Weerdt 1981, 1984; Lewis 1989) that are influenced by numerous inter-related abiotic factors such as available light (Stromgren 1976), current and water clarity (Weerdt 1981). Given their plasticity and the lack of definitive characters that might be used to facilitate identification, it seems appropriate to collect information on a range of variables.

There has been little work on the species of *Millepora* occurring in Brazil. Laborel (1970) showed that there are some problems with their identification and suggested that Verrill (1868) and Boschma (1948a) incorrectly identified *M. nitida* (Verrill, 1868) as *M. alcicornis* (Linnaeus 1758) and *M. alcicornis* as *M. braziliensis* (Verrill 1868), respectively. In other studies, Boschma (1962) and Weerdt (1990) showed that *M. squarrosa* (Lamarck, 1816) and *M. braziliensis* co-exist across Brazilian reefs, although it is possible that the species identified as *M. squarrosa* by Weerdt (1990) may have been *M. braziliensis* (Amaral 1995, 1997; Amaral et al. 1997, 1998a). Given the lack of information describing species of *Millepora* and their taxonomy across Brazilian reefs, our aims in this study were to identify the various species and provide a preliminary overview of their skeletal morphometry. In addition, because of possible confusion in taxonomy between *M. squarrosa* and *M. braziliensis,* we compared local specimens of *M. braziliensis* with specimens of *M. squarrosa* from the Caribbean.

Materials and Methods

This study was done using a total of 112 colonies of *Millepora,* including 103 colonies collected from various reef sites along the Brazilian coast (Fig. 1) and 9 colonies of *M. squarrosa* from the National Museum of Natural History at the Smithsonian Institution (originally collected from Martinique, Puerto Rico, St. Lucia, Guadeloupe and Grenada in the Caribbean). The Brazilian specimens are currently stored at the Invertebrate Department of the National Museum of Rio de Janeiro, the Systematic and Ecology Department of the Federal University of Paraíba, and the Laboratory of Reef Environment at the Federal Rural University of Pernambuco.

The Brazilian colonies were collected at various sites (see Fig. 1) from depths down to 35 m and immediately placed in labeled plastic bags for transportation to the laboratory. Coralla were cleaned in a solution of 30% sodium hypochlorite, dried, and analyzed under a stereoscopic microscope equipped with an ocular micrometer. Data

Fig. 1. Locations of reef sites from which specimens were collected in Brazil.

collected from all samples included: growth form; height and transverse diameter of the colony; characteristics of the upper part of the colony; number and diameter of the principal and terminal branches; form, density and diameter of the dactylopores and gastropores (a minimum of 18 replicate measurements); surface texture of the colony; distribution of the pores in several parts of the colony; presence or absence of ampullae and their diameter; and numbers of epibionts and cyclosystems.

Analyses of data.—Quantitative delineation among species was done with regard to various skeletal characteristics, referenced against descriptions provided in previous studies of *Millepora* (e.g., Boschma 1962, Weerdt 1981). To provide some assessment of intra- and inter-specific variabilities in morphology, where there were sufficient data (i.e., at least two specimens of each species from the various locations), the diameter of dactylopores and gastropores of species were compared in separate balanced, nested analyses of variance (ANOVA) (Underwood 1981). Prior to analyses, data were tested for heteroscedasticity using Cochran's test (Winer 1971) and then transformed if necessary. Using the available data, 4 analyses were done including: a one-nested factor ANOVA for *M. alcicornis, M. braziliensis* and *M. nitida* at the Abrolhos Islands; a two-factor nested ANOVA for *M. alcicornis* and *M. braziliensis* at three locations in Brazil (Maceió, Japaratinga and Tamandaré); and a one-nested factor ANOVA for *M. squarrosa* at three locations in the Caribbean. Because *M. braziliensis* and *M. squarrosa* showed no significant spatial variability in mean diameters of dactylopores and gastropores among their respective locations (e.g., in Brazil and the Caribbean—see Results), 5 specimens of each were randomly selected across all locations and analyzed with 5 specimens of *Millepora* sp. a from Manuel Luiz Parcel in a one-nested factor ANOVA. Means were separated following significant *f*-tests using the Student-Newman-Keuls (SNK) test (Underwood 1981).

Results

Quantitative delineation among species: Based on differences in growth form and skeletal characteristics, the 103 colonies collected from Brazil were separated into 4 species: *M. alcicornis* (34 colonies—Figs. 2, 3), *M. braziliensis* (45 colonies—Fig. 2), *M. nitida* (13 colonies—Figs. 2, 3) and *Millepora* sp. a (11 colonies—Fig. 2) (Tables 1, 2).

Millepora alcicornis (Figs. 2 and 3) was identified at 9 locations from Cabo Frio in the south to Manuel Luiz Parcel in the north and was easily distinguished from its congenerics (Fig. 1 and Table 1). In most colonies, the growth form typically was finely ramified, varying to totally incrusted, whereas surface textures were irregular having shallow ampullae (Table 1). The dactylopores and gastropores were predominantly rounded and larger than those in all other species examined (see Results below) (Table 2). *M. alcicornis* also had the greatest mean numbers of epibionts (mostly *Megabalanus stultus*), gastropores per cm^2, and ampullae (Table 2). Additional characteristics that distinguished *M. alcicornis* from its cogenerics included the presence of gorgonians as substratum in some colonies and relatively fewer cyclosystems per cm^2.

Millepora braziliensis (Fig. 2) showed a similar spatial diversity as *M. alcicornis,* occurring at 9 locations from Guarapari in the south to Manuel Luiz Parcel in the north (Fig. 1, Table 1). Unlike other species of *Millepora* from Brazil, the growth form in most colonies typically was honey-combed, comprising several different types including ramified, hemispheric, columnar, laminate, fan forms and totally incrusted colonies (Table 1). *M. braziliensis* had a very irregular surface texture, ampullae that varied from shallow to deep (Table 1), and the greatest mean number of dactylopores per gastropore (Table 2). The mean diameters of gastropores and dactylopores were similar to *M. nitida* (Table 2).

Millepora nitida (Figs. 2, 3) was identified at the Abrolhos Islands and Maceió (Fig. 1, Table 1). Its predominant growth form was ramified with short and round branches, although in some colonies hemispheric forms were also observed (Table 1). Surface texture was smooth, with few cirripeds (Table 1). *Millepora nitida* had shallow and isolated ampullae, comparable mean diameters of gastropores and dactylopores to *M. braziliensis* and a similar mean ratio of dactylopores per gastropore (Table 2). Unlike *M. alcicornis* and *M. braziliensis,* the form of the pores was predominantly irregular (i.e., not circular) (Table 1). Compared to all other species examined, *M. nitida* showed a greater transverse diameter, an intermediate colony height, and had greater and fewer mean numbers of cyclosystems and gastropores per cm^2, respectively.

Millepora sp. a (Fig. 2) was identified only at Manuel Luiz Parcel, but was very abundant in this region. The species was brown and grew in the form of pillars or fans at a depth of 30–32 m. Nearly all colonies examined were bleached and many incrusted with algae. Unlike the other species examined, *Millepora* sp. a had a growth form that was always columnar (average height of 162.7 mm) and a comparatively smoother and flatter texture (Tables 1 and 2). The density of gastropores was

Table 1.—Qualitative characters of the 5 *Millepora* species studied.

Character	*M. alcicornis* (34 colonies)	*M. braziliensis* (45 colonies)	*M. nitida* (13 colonies)	*Millepora* sp. a (11 colonies)	*M. squarrosa* (9 colonies)
Location of specimens (*n*)	Manuel Luiz Parcel (1) Atol das Rocas (1) João Pessoa (3) Tamandaré (4) Japaratinga (3) Maceió (5) Abrolhos Islands (7) Guarapari (2) Cabo Frio (8)	Manuel Luiz Parcel (1) João Pessoa (3) Serrambi (2) Tamandaré (5) Maragogi (4) Japaratinga (8) Maceió (15) Abrolhos Islands (4) Guarapari (3)	Maceió (1) Abrolhos Islands (12)	Manuel Luiz Parcel (9)	Caribbean (9)
Predominant growth form	Ramified (mostly), hemispherical and columnar	Honey-combed (mostly) and columnar	Ramified with rounded branches and hemispherical	Columnar	Honey-combed
Superior part of colony	Ramified	Honey-combed	Ramified with rounded branches	Sharp	Honey-combed
Surface texture	Irregular	Very irregular	Smooth	Very smooth	Irregular
Ampullae	Shallow	Varying between deep and shallow	Shallow and isolated	Shallow and rare	Shallow and rare
Dactylopore form	Predominantly rounded	Predominantly rounded	Predominantly deformed	Very shallow	Predominantly rounded
Gastropore form	Predominantly rounded	Predominantly rounded	Predominantly deformed	Very shallow	Predominantly rounded
Epibionts	Many cirripeds	Some cirripeds	Few cirripeds	No cirripeds	Few cirripeds
Substratum	Calcareous algae, mud or gorgonians	Calcareous algae, Scleractina, *Agaricia agaricites* or mud	Calcareous algae, Scleractina, *Agaricia agaricites*	Calcareous algae and bryozoans	Calcareous algae

Table 2.—Means (±*SE*) [number of measurements pooled across specimens] of various skeletal characters from the 5 *Millepora* species. (—) = the characteristic was not recorded, Dia = diameter, No = number. All measurements are in mm.

Characteristic	*M. alcicornis* (34 colonies)	*M. braziliensis* (45 colonies)	*M. nitida* (13 colonies)	*Millepora* sp. a (11 colonies)	*M. squarrosa* (9 colonies)
Height of colony	138.20 (11.31) [23]	109.00 (7.04) [41]	102.70 (8.96) [13]	162.70 (15.52) [11]	60.90 (7.67) [9]
Transverse diameter	103.60 (8.82) [22]	102.10 (5.73) [35]	129.30 (10.51) [13]	83.78 (11.98) [11]	61.70 (5.64) [9]
No principal branches	1.90 (0.22) [23]	3.20 (0.62) [16]	1.40 (0.30) [10]	1.00 (0.00) [11]	—
Dia of principal branch	22.85 (1.913) [26]	20.20 (2.63) [50]	84.10 (8.45) [15]	—	—
Dia of terminal branch	6.65 (0.34) [491]	24.60 (1.56) [144]	11.55 (0.93) [72]	—	—
No of ampullae	11.08 (2.08) [23]	6.50 (1.41) [23]	10.60 (7.94) [6]	1.00 (0.00) [1]	2.00 (0.00) [1]
Dia of ampullae	0.41 (0.02) [171]	0.53 (0.01) [136]	0.45 (0.02) [22]	0.36 (0.03) [11]	—
No of cyclosystems	1.10 (0.037) [32]	2.00 (0.10) [38]	2.10 (0.07) [11]	1.45 (0.21) [11]	1.60 (0.073) [9]
No of epibionts	16.80 (5.18) [12]	5.40 (2.07) [14]	5.40 (2.64) [7]	—	—
Dactylopores per gastropore	5.20 (0.13) [8]	7.75 (0.72) [4]	6.80 (0.14) [6]	6.30 (0.41) [11]	6.50 (0.50) [4]
Dia of dactylopores	0.14 (0.001) [872]	0.10 (0.001) [1130]	0.10 (0.002) [240]	0.08 (0.002) [200]	0.07 (0.002) [166]
Dia of gastropores	0.29 (0.002) [827]	0.25 (0.001) [1152]	0.24 (0.003) [259]	0.11 (0.004) [203]	0.22 (0.003) [187]
No of gastropores per cm^2	29.25 (3.17) [35]	18.15 (1.41) [39]	11.00 (1.00) [12]	23.27 (2.54) [11]	21.30 (2.49) [9]

23.3 per cm^2 and therefore similar to *M. alcicornis. Millepora* sp. a had similar sized dactylopores as *M. squarrosa*; however, the mean diameter of the gastropores was considerably less (see Results below). Compared to the majority of other species examined, the mean number of dactylopores per gastropore was intermediate, whereas ampullae were substantially smaller and fewer (Table 2).

Intra- and inter-specific variation among diameters of dactylopores and gastropores: Significant differences were detected among specimens in all analyses, indicating substantial intra-specific variability. Significant differences were detected between *M. nitida, M. braziliensis* and *M. alcicornis* collected from the Abrolhos Islands, for the diameter of the dactylopores, but not the gastropores (Fig. 4A, B, Table 3). Student-Newman-Keuls tests showed that compared to *M. nitida* and *M. braziliensis, M. alcicornis* had dactylopores with a significantly greater mean diameter (Fig. 4A).

Two-factor nested ANOVA examining the differences in diameter of gastropores and dactylopores between *M. braziliensis* and *M. alcicornis* at three locations (Maceió, Japaratinga and Tamandaré) detected significant differences in diameter of gastropores and an interaction between location and species of *Millepora* for diameter of dactylopores (Table 4). SNK tests of these data showed that compared to *M. braziliensis, M. alcicornis* had a greater mean diameter of dactylopores at Tamandaré and Maceió and a significantly greater mean diameter of gastropores at all locations (Fig. 5A, B, Table 4). *Millepora braziliensis* showed no significant differences in diameter of dactylopores across the three locations (Fig. 5A).

One-nested factor ANOVA examining differences in the diameters of gastropores and dactylopores of *M. squarrosa* (Fig. 2) at three locations in the Caribbean (St. Lucia, Guadeloupe and Grenada) failed to detect any significant differences due to location (Table 5). Subsequent analysis of

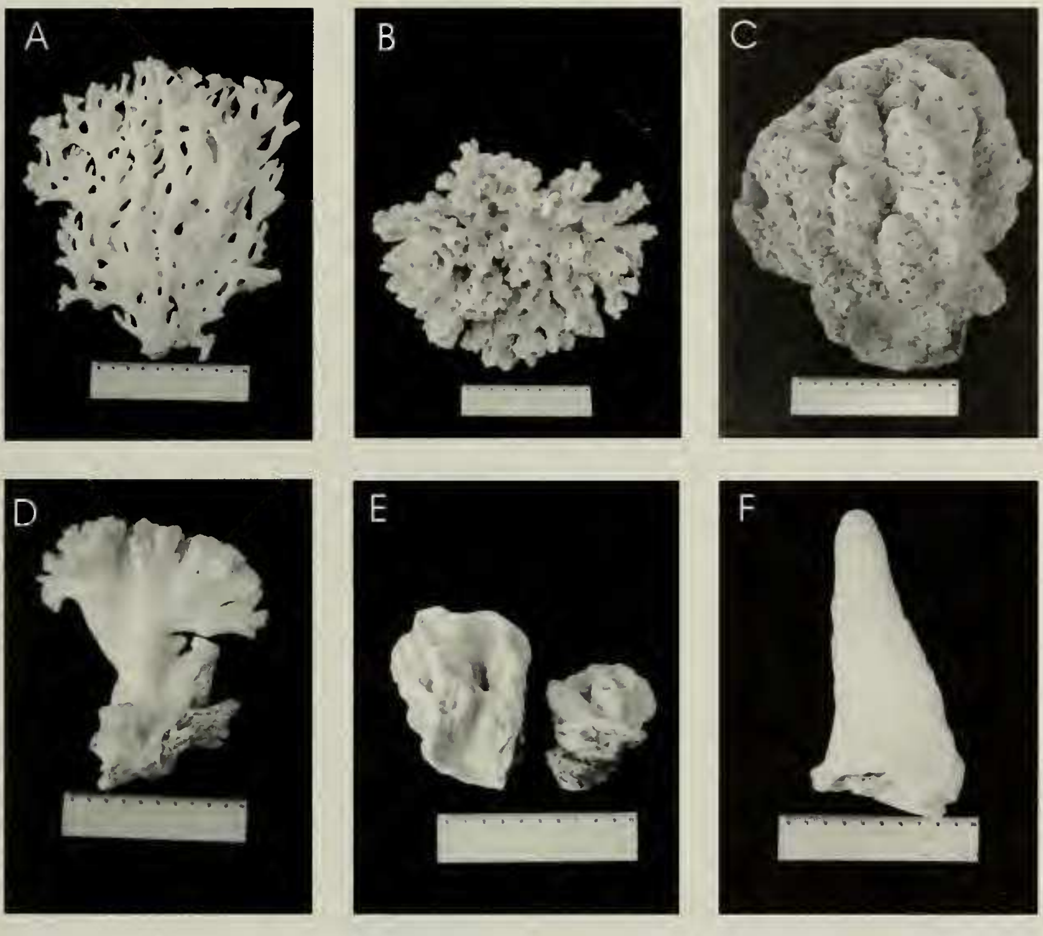

Fig. 2. Photographs of (A) ramified *Millepora alcicornis,* (B) ramified *M. braziliensis,* (C) honey-combed *M. braziliensis,* (D) ramified *M. nitida,* (E) honey-combed *M. squarrosa,* and (F) columnar *Millepora* sp. a.

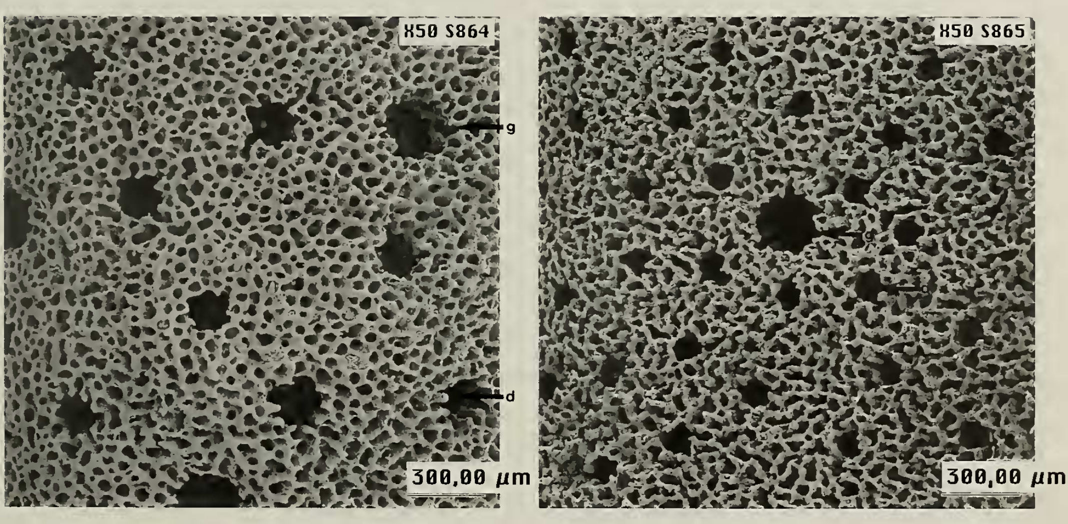

Fig. 3. Scanning microscopy of *Millepora alcicornis* (left) and *M. nitida* (right).

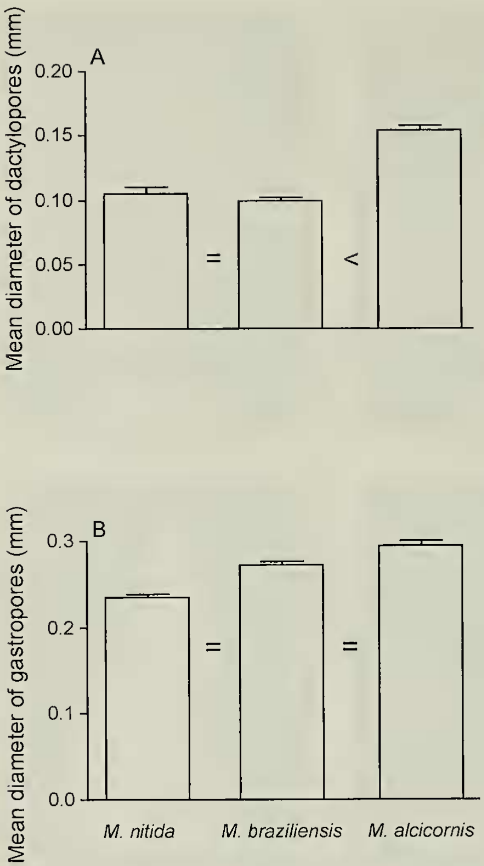

Fig. 4. Differences in mean diameter (±*SE*) for (A) dactylopores and (B) gastropores of *M. nitida, M. braziliensis* and *M. alcicornis* at the Abrolhos Islands. < represents significant differences detected in SNK tests.

these specimens with *M. braziliensis* and *Millepora* sp. a pooled across their respective locations detected significant differences in mean diameter of gastropores, but not dactylopores (Fig. 6A, B, Table 6). SNK tests showed that *Millepora* sp. a had a significantly smaller mean diameter of gastropores than *M. braziliensis* and *M. squarrosa* (Fig. 6B).

Discussion

The identification of *Millepora* species collected in this study was based on various morphological characteristics, including diameters of the gastropores and dactylopores. From the morphological observations made and the various significant differences detected, it is apparent that, like the results from previous studies (e.g., Boschma 1948a; Weerdt 1981, 1984; Amaral 1997), *Millepora* shows considerable intra-specific variability. As the synonymy lists are very extensive, we suggest that Boschma (1948a) be consulted for more details on *M. alcicornis* and *M. braziliensis* and Verrill (1868) for *M. nitida* as suggested by Weerdt (1984). Despite their high phenotypic plasticity, sufficient information was collected to facilitate separation of the collected colonies into four species: *M. alcicornis, M. braziliensis, M. nitida* and *Millepora* sp. a.

Laborel (1970) observed that *M. alcicornis* is an important reef building component off northeast Brazil (e.g., at Tamandaré 8°41′S, 35°05′W, where it forms a great part of the reef structure), occurring to depths of 15 m. The results from this study show that the geographical distribution of *M. alcicornis* is extended to Manuel Luiz Parcel (0°46′S, 44°5′W) (see also Amaral et al. 1998b, 2000) and that its bathymetric limit off Brazil is at least 30 m (based on samples collected at Manuel Luiz Parcel). This

Table 3.—Summaries of *f*-ratios from one-nested factor analysis of variance to investigate differences in the diameter (mm) of gastropores and dactylopores between *M. braziliensis, M. nitida* and *M. alcicornis* at the Abrolhos Islands. ** significant ($P < 0.01$), * significant ($P < 0.05$).

		Diameter (mm)	
Source of variation	*df*	Gastropores	Dactylopores
Species of *Millepora* = Sm	2	1.94	6.61*
Specimens(Sm) = S(Sm)	6	34.49**	20.23**
Residual	171		

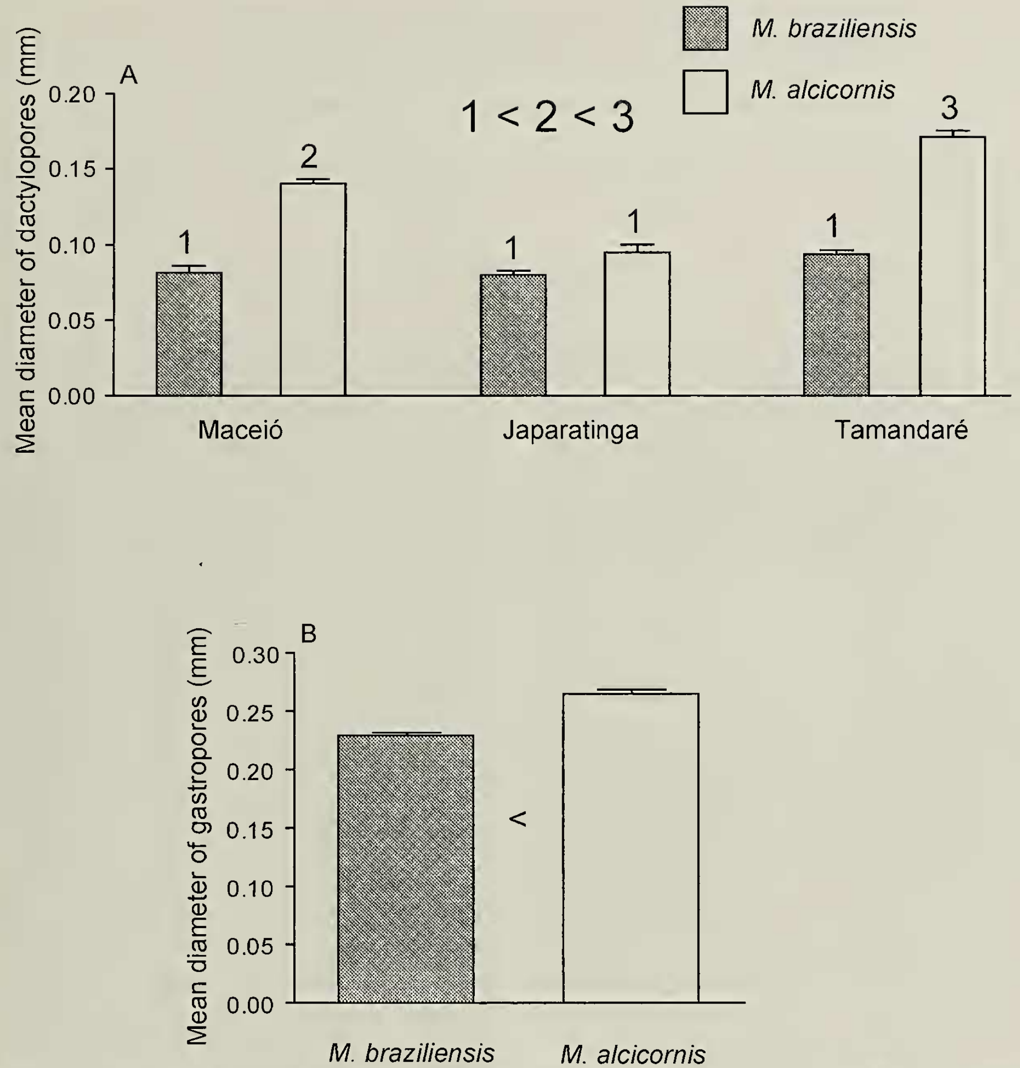

Fig. 5. Differences in mean diameter (±*SE*) for (A) dactylopores and (B) gastropores of *M. alcicornis* and *M. braziliensis* across three locations in Northeast Brazil. < represents significant differences detected in SNK tests.

Table 4.—Summaries of *f*-ratios from two-factor nested analysis of variance to investigate differences in the diameter (mm) of gastropores and dactylopores (data were sqrt(x + 1) transformed) between *M. braziliensis*, and *M. alcicornis* at three locations in northeastern Brazil (Maceió, Japaratinga and Tamandaré). ** significant ($P < 0.01$), * significant ($P < 0.05$).

Source of variation	*df*	Diameter (mm)	
		Gastropores	Dactylopores
Location = L	2	5.36*	16.20**
Species of *Millepora* = Sm	1	75.33*	7.57
L × Sm	2	0.14	8.40**
Specimens(L × Sm) = S((L × Sm)	12	20.63**	9.50**
Residual	171		

Table 5.—Summaries of *f*-ratios from one-nested factor analysis of variance to investigate differences in the diameter (mm) of gastropores (data were ln(x + 1) transformed) and dactylopores of *M. squarrosa* at three locations (St. Lucia, Guadeloupe and Grenada) in the Caribbean. ** significant ($P < 0.01$).

Source of variation	*df*	Diameter (mm)	
		Gastropores	Dactylopores
Location = L	2	3.10	0.06
Specimens(L) = S(L)	3	12.17**	20.58**
Residual	102		

depth is still within the limits proposed by Lewis (1989) (i.e., 50 m).

Boschma (1948b) affirmed that *M. alcicornis* is a species with an extremely variable growth form, having branches divided in ramifications, which generally are compressed. In this study, we observed variation in growth forms of *M. alcicornis,* including fine and thick ramified branches as well as totally incrusting colonies. Weerdt (1984) also considered the growth form as being ramified, with delicate or thick branches often united by plates and flattened in the extremities. Using specimens collected from the Caribbean, Weerdt (1984) defined the surface texture of *M. alcicornis* as flat. Gastropores and dactylopores were studied in six colonies and observed to vary from 0.15 to 0.30 mm and from 0.06 to 0.17 mm, in diameter, respectively, whereas the density of gastropores was low, varying from 5 to 50 per cm^2. In contrast, we observed the surface texture as being intermediate, varying from flat (majority of colonies) to wrinkled (few colonies). Gastropores and dactylopores had average diameters of 0.29 and 0.1 mm, respectively, whereas the gastropore density ranged from 4 to 84 per cm^2, with a mean of 29.3 per cm^2 (Table 2). The differences between the results of Weerdt (1984) and this study might be attributed to sample size (i.e., 6 versus 34 colonies, respectively), or may be due to the influences of different ecological conditions between the Caribbean and Brazil.

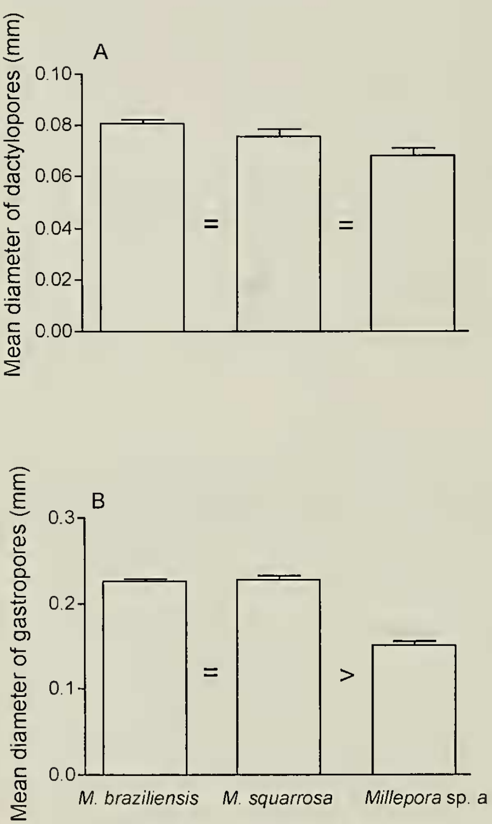

Fig. 6. Differences in mean diameter (±*SE*) for (A) dactylopores and (B) gastropores of *M. braziliensis, M. squarrosa* and *Millepora* sp. a pooled across all locations. > represents significant differences detected in SNK tests.

According to Boschma (1949b), the diameters of the ampullae of two colonies of *M. alcicornis* varied from 0.3 to 0.45 mm and from 0.5 to 0.7 mm. In this study, ampullae were observed in ⅔ of the colonies, with a mean of 11.08 ampullae per colony and diameters that ranged from 0.25 to 1.33 mm, with an average of 0.41 mm (Table 2). This species had the greatest number of epi-

Table 6.—Summaries of *f*-ratios from one-nested factor analysis of variance to investigate differences in the diameter of gastropores and dactylopores between *M. braziliensis, M. squarrosa* and *Millepora* sp. a pooled across their respective locations. ** significant ($P < 0.01$).

Source of variation	*df*	Diameter (mm)	
		Gastropores	Dactylopores
Species of *Millepora* = Sm	2	14.21**	0.91
Specimens(Sm) = S(Sm)	12	17.59**	12.76**
Residual	253		

bionts (mostly the barnacle *Megabalanus stultus*), similar to the observation made by Lewis (1992) for *M. complanata.*

Laborel (1970) suggested that like *M. alcicornis, M. braziliensis* is an important reef building component in Brazil and noted colonies with diameters of between 2 and 3 m. The growth form occurring in sheltered sites was observed to be arborescent. In more exposed sites, colonies revealed a more massive honey-combed form, whereas in very calm sites morphology varied from laminate and fine branching, similar to *M. complanata* and *M. squarrosa.* Although the size of colonies observed by Laborel (1970) were substantiated herein, the latter observations were not confirmed. For example, the majority of colonies of this species collected from only one part of a reef at Tamandaré had several different growth forms. The results presented here have shown that the geographical distribution of *M. braziliensis* is extended to Manuel Luiz Parcel (00°46′S and 44°15′W) (see also Amaral et al. 1998b, 2000).

According to Boschma (1962), *M. braziliensis* contains comparatively fine ramifications which, in its upper parts, are divided into a certain number of short lateral branches radiating in several directions. Boschma (1962) also found other colonies of hemispheric or globular form, bearing a great number of close and fine branches, with round extremities. *Millepora braziliensis* examined in this study had various growth forms, including: honey-combed (found in the majority of the colonies), ramified honey-combed, hemispheric honey-combed, ramified hemispheric, hemispheric to laminate, ramified columnar, columnar to laminate, flat laminate, ramified thick, fan-like, and colonies totally incrusting (Table 1). Boschma (1962) mentioned two colonies that had heights of 14.5 and 13 cm and large transverse diameters of 7 and 19 cm, respectively. The holotype is 7.3 cm in height and has a transverse diameter of 3.2 cm (Boschma 1962). The results obtained in this study (from 45 colonies) extend this variability (e.g., mean height and transverse diameter were 10.9 cm and 10.2 cm, respectively; see Table 2). Boschma (1962) found a great number of ampullae in this species, with diameters that varied from 0.3 to 0.4 mm. Of the 45 colonies studied here, 23 had ampullae with an average of 6.5 ampullae per specimen and a mean diameter of 0.53 mm (Table 2).

There was clear delineation between *M. braziliensis* and *M. alcicornis* in relation to the gastropores at the coastal locations examined, with *M. alcicornis* having a greater mean diameter of gastropores (Fig. 5 and Table 4). However, no significant difference was detected for the diameter of the gastropores between these species at the Abrolhos Islands: only the dactylopores were significantly larger in *M. alcicornis* than in the other studied *Millepora* (Fig. 4, Table 3). One possible explanation for this result is the better water quality and environmental conditions at the Abrolhos Islands. For example, higher sedimentation rates (or pollution) in coastal localities may have a greater effect on the development of gastrozooids of *M. alcicornis* than *M. braziliensis.*

We compared *M. braziliensis* and *Millepora* sp. a from Brazil and *M. squarrosa* from the Caribbean, after first testing for intra-specific differences among respective distributions of *M. braziliensis* and *M. squarrosa*. Despite no significant differences in diameters of the gastropores and dactylopores between *M. braziliensis* and *M. squarrosa* (Fig. 6), the observed morphological differences, including number of ampullae, dactylopores per gastropore and number of gastropores per cm^2 provide some evidence to suggest that these species should be considered separate. However, to eliminate doubts over their synonymy, we suggest the use of molecular systematics studies (i.e., using DNA and isoenzymes). SNK tests did detect significant differences between these two species and *M.* sp. a, with the latter having a significantly smaller mean diameter of gastropores (Fig. 6, Table 6). Combined with the other qualitative and skeletal characters recorded (Tables 1, 2), this result provides some evidence to suggest that *Millepora* sp. a from Manuel Luiz Parcel is a new species; however, its status should also be confirmed via molecular systematics studies.

Laborel (1970) noted that *M. nitida* had a dense and compact skeleton and should be considered endemic to the state of Bahia (17°20′S, 038°35′W). The results presented here have shown that the geographical distribution of *M. nitida* is extended to the reefs of Ponta Verde (Alagoas State). Boschma (1962) found that *M. nitida* forms a round mass of close, fine branches, which possess lateral branches, each of these dividing into smaller branches. The external parts of the branches are rounded, cylindrical or slightly compressed and surface texture considered flat. Similarly, in this study, the predominant growth from of *M. nitida* was observed as being ramified with short and rounded branches, but hemispheric forms were also collected. With regard to the dimensions of the colonies, Boschma (1962) observed colonies with heights of 8.5 cm, 6.8 cm, and 3.8 cm and respective transverse diameters of 11, 11.5, 6.7 and 4.3 cm. We examined 13 colonies of this species and enlarged the variation of mean height and transverse diameter to 10.3 and 12.9 cm, respectively (Table 2).

The results from this study have shown that Brazilian *Millepora* colonies with totally incrusting forms can be identified based on their coenosteal pores. However, identification of *Millepora* based on growth form alone contains much imprecision, primarily because intermediate forms frequently occur, making it almost impossible to identify incrusting colonies (Amaral 1997). In such cases it is necessary to study other characters to facilitate identification. According to Boschma (1948a) and Weerdt (1981), incrusting colonies that conform to the shape of their substrata don't exhibit enough characters for a specific identification. Nevertheless, several authors continued to define the species of *Millepora* based on growth form of the colony and geographical distribution (e.g., Boschma 1948a, 1948b, 1961, 1962, 1966; Stearn & Riding 1973; Weerdt 1981, 1984, 1990). In a revision of taxonomic problems with this genus, Weerdt (1981, 1984) emphasized the need for additional characters and acknowledged a shortage of holotypes and the lack of ecological data associated with specimens in museum collections.

Since last century, Boschma (1948b) considered that the specific characters should be those related to growth form of the colony. Other skeletal characters, such as size and density of the gastropores and dactylopores, were intensely studied in the past, but were considered insufficient because of high intra-specific variability (Boschma 1948a, 1948b, 1949a, 1950, 1964). Despite this, we showed that these characters were beneficial in separating some of the Brazilian species. Other characters have been used in *Millepora* systematics with varying degrees of success. These characters include: the morphology of the zooids (Kruijf 1975), ampullae and medusae (Lewis 1991), the density and diameter of the zooxanthellae (Amaral & Costa 1998), and isoenzymes (Manchenko et al. 1993, Amaral et al. 1997). Moshchenko (1993) studied *M. platyphylla* and *M. dichotoma* and found that the zooids, ampullae, coenosarc, gastropores and dactylopores were similar in ramified and laminate *Millepora* and that these characters could not be used in taxonomic studies. In later work, Moshchenko (1994, 1995) applied a quantitative method of estimating the structure of the pores and found that the pores of laminate *Millepora* were different from those of ramified colonies and more specifically, that the pores of *M. platyphylla* were characteristically different from ramified *Millepora* (Moshchenko 1995). According to Moshchenko (1996), only two species of *Millepora* could undoubtedly be distinguished in the Indo-Pacific region: *M. platyphylla* and *M. dichotoma*.

Given the above and the results from this study, it is apparent that a range of variables are required to facilitate taxonomy of *Millepora* and that in some cases, the use of only growth form and attributes of the gastropores and dactylopores is unlikely to be sufficient. Whereas it may be feasible to examine other morphological characteristics (such as those discussed above) to aid delineation among species, studies involving molecular systematics may be required to confirm identification.

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